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FURTHER EXPERIMENTS ON INHERITANCE IN MAIZE

BY

H. K. HAYES and E. M. EAST.

CONNECTICUT AGRICULTURAL EXPERIMENT STATION.

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FURTHER EXPERIMENTS ON INHERITANCE IN MAIZE.

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H. K. Hayes * and E. M. East.

This paper is a report on the inheritance of certain differences in the endosperm of various maize races that have been made the basis of a division into the subspecies *everta, indurata, indentata* and *amylacea.* To these investigations, a genetic study of the shape of seed which characterizes the socalled rice pop corns is added.

The writers take pleasure in acknowledging the efficient aid of Mr. A. F. Schultze, assistant botanist at the Connecticut Agricultural College, and Mr. C. D. Hubbell, assistant at the Connecticut Agricultural Experiment Station, in the considerable amount of field work involved.

MATERIAL AND METHODS.

The parental races used in the crosses were self-fertilized for several years before any hybrids were made, and are believed to have been homozygous for the characters studied. The material from which these races originated was described in a previous publication (See East and Hayes, 1911), but the following additional points regarding it should be noted:

1. *Zea mays everta.* The pop corns.

No. 64. White rice pop.

This white pop is one of the lines which has been produced from No. 23, (East & Hayes, 1911). It breeds true to the "rice" type of seed,—sharply pointed where the style

* Mr. Hayes resigned January 1, 1914, to take charge of plant breeding work in the Experiment Station and College of Agriculture of the University of Minnesota. The experimental work here reported was carried on at the Connecticut Station as an Adams Fund Project. The Minnesota Experiment Station and the Bussey Institution of Harvard, should be given credit for time spent in the preparation of this paper for publication.

(silk) was attached,—although there is some variation in the degree to which this character is expressed. The seeds contain only very small amounts of soft starch.

No. 65. A white, flint-like pop.

This is a strain produced from No. 26, of our previous publication. Its seeds resemble those of a typical flint variety in shape, and contain only very small amounts of soft starch.

2. *Zea mays indurata.* The flint corns.

No. 5. Watson's white flint.

This variety is a true white flint which developes a red pericarp in full sunlight. The depth of tint which developes naturally is therefore inversely proportional to the thickness of the husk. The seeds contain a larger proportion of corneous starch than many races of flint corn, though less than that shown by the two pop varieties just described. As in all flints, however, there is a small zone of soft starch in the center of the seed.

3. *Zea mays indentata.* The dent corns.

No. 6. Leaming dent.

This is a vigorous strain of a famous yellow dent. Like all varieties of its group, the soft starch extends over the whole summit of the seeds, yet the layer is thin enough to allow the race to be classified as a smooth dent (i. e. not beaked).

4. *Zea mays amylacea.* The flour corns.

No. 10. White flour.

This is a floury race with seeds resembling the average 8 rowed flint in shape. Though the seeds usually contain only floury starch, sometimes an almost imperceptible layer of corneous starch developes in the exterior of the endosperm. It seems likely that this variation is an effect of external conditions rather than of gametic impurity.

The plantings have always been made from the original seed envelope, and pains have been taken to prevent the misplacement of seeds.

The different families were marked in the field by heavy stakes to which wired tree labels were attached, but to prevent error through their misplacement a planting plan was made each year showing the exact location and the number of hills of each strain.

Classification of seeds was made only from hand pollinated ears, although the remaining ears of a selection were always examined, and in the case of those seed characters not immediately affected by pollination, were used in determining the range of variation.

The various races were given different numbers as No. 10 flour corn and No. 5 flint corn. A cross between 10 and 5 was then written as 10 x 5 the female parent appearing first. Different self-pollinated ears obtained from growing the cross between (10 x 5) were labeled (10 x 5)-1, (10 x 5)-2, etc. Later generations were labeled as (10 x 5)-1-2, (10 x 5)-1-3, (10 x 5)-2-4, etc. If the F_1 generation was pollinated with pollen from the flint parent, this ear received the label (10 x 5)-1 x (5-2)-8-3, as the case might be. This back cross was planted the following year as (10 x 5 x 5). Thus we had complete records of the parents and ancestry of our various lines.

The field technique has been described in previous publications.

For convenience the various crosses will be considered under special headings.

Family (10 x 5), Flour x Flint.

A cross between the floury race No. 10 and flint race No. 5 was made in 1910, the resulting seeds resembling the female parent. As indicated above, the characteristic difference between these races is the amount of soft starch in the seeds. The flint race produces a small quantity of soft starch in the center of the seed, surrounded by a large layer of corneous starch, while the flour race produces only an occasional trace of corneous starch around the exterior of the endosperm. No immediate effect of pollination through double fertilization was expected, as both our own earlier results and those of other investigators (Correns and Lock) were thought to imply that these differences in the starchy character of the endosperm behaved in heredity as if they pertained to the plant rather than to the endosperm. On growing this cross in 1910, however, we were much surprised to find a clear segregation of seeds on each ear. This fact showed that the physical condition of the starch in these races

was not a maternal character, since in that case we should have expected a uniform population of seeds on the F_1 ears, resembling either the male or female parents or intermediate between them.

A classification of the seeds from the ears of the F_1 generation plants, is given in Table 1. Only two classes could be made; corneous seeds like the flint parent, and floury seeds resembling the floury parent. There was no difficulty in dividing the seeds into these two classes. Of the thirteen ears shown in Table 1, some contained a greater proportion of flint or of floury seeds than others, but all gave close approximations to a 1 to 1 ratio. This being a novel F_1 ratio, further experiments were made to find a genetic interpretation of it.

TABLE 1.

Self-pollinated Ears from the F_1 Generation of a Cross Between No. 10 Flour and No. 5 Corneous Flint.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5)-1	145	186
" -3	208	142
" -4	169	161
" -5	156	169
" -6	181	166
" -7	189	172
" -8	175	203
" -9	168	165
" -10	213	213
" -11	209	205
" -12	238	237
" -13	190	197
" -14	252	223
Total	2493	2439

The floury seeds of (10 x 5)-7 and (10 x 5)-8 were labeled (10 x 5)-7S and (10 x 5)-8S to distinguish them from the corneous (flint-like) seeds of the same ears, which were labeled (10 x 5)-7C and (10 x 5)-8C respectively. The data from sev-

[1] The word hybrid in these discussions is used in a peculiar sense to avoid longer descriptions. It means a cob bearing a population of seeds belonging to more than one phenotype.

eral self-fertilized ears obtained by growing the floury seeds are given in Table 2. Of a total of 11 hand-pollinated ears, 8 were hybrid[1], and gave 1 to 1 ratios with a total of 748 corneous to 691 floury seeds. The other 3 ears bred true for the floury habit.

Of the open field or naturally pollinated ears, 28 were hybrids and 23 pure floury. This gives a total of 36 hybrids to 26 pure floury, which, considering the number grown, is a reasonable approximation of a 1 to 1 ratio.

TABLE 2.

SELF-POLLINATED EARS OBTAINED THROUGH GROWING FLOURY SEEDS OF EARS (10 x 5)-7 AND (10 x 5)-8.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5)-7 S-1	108	125
" -7 S-2	76	59
" -7 S-4	162	126
" -7 S-7	58	55
" -8 S-5	100	97
" -8 S-6	53	48
" -8 S-7	91	89
" -8 S-8	100	92
" -8 S-2		Pure Floury
" -8 S-3		" "
" -8 S-4		" "
Total in hybrid ears	748	691

Table 3 gives the results of planting the corneous seeds of ears (10 x 5)-7 and (10 x 5)-8. Of a total of 9 self-fertilized ears, 5 proved to be hybrids and 4 were pure corneous. The ratio of corneous to floury seeds in these 5 hybrid ears was 464 corneous to 482 floury, a close approximation of 1 to 1. Of the open field ears 38 were corneous and 34 hybrids. Thus in this case the hybrid and the pure corneous ears are clearly in a 1 to 1 ratio.

TABLE 3.

Self-pollinated Ears Obtained Through Growing Corneous Seeds of Ears (10 x 5)-7 and (10 x 5)-8.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5)-7C-6	30	29
" -7C-9	73	101
" -8C-3	97	81
" -8C-8	191	211
" -8C-10	73	60
" -7C-5	Pure corneous	
" -7C-8	" "	
" -8C-5	" "	
" -8C-6	" "	
Total in hybrid ears	464	482

Table 4 gives the results of pollinating ears of the F_1 plants with pollen from the parental strains No. 10 flour, and No. 5 flint, respectively. Only 1 ear was obtained from the back cross between (10 x 5) and the No. 10 parent. This ear had 156 corneous and 184 floury seeds. Three ears resulted from crossing plants of (10 x 5) with the flint, or No. 5 parent. These ears showed various ratios of corneous to floury seeds, but the deviations from 1: 1 ratios were not all in the same direction. Of the total number of seeds in the four ears, 544 were corneous and 543 floury.

TABLE 4.

Ears of the First Generation Cross of (10 x 5) Pollinated With Pollen From the Pure Parents, No. 10 Flour and No. 5 Corneous Flint.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5)-13 x (10-3)-14	156	184
" - 3 x (5-3)-1	102	79
" - 1 x (5-3)-3	107	79
" - 5 x (-5-3)-7	179	201
Total	544	543

Table 5 gives the results obtained from planting floury seeds of ears (10 x 5)-5 x (5-3)-7 and (10 x 5)-1 x (5-3)-3 of Table 4. It was expected that such seeds would be hybrids between the corneous and floury types and should therefore give hybrid ratios when grown. The table shows 10 self-pollinated ears which gave a ratio of 1014 corneous to 850 floury seeds. Seventy-nine naturally pollinated ears were all hybrids showing a definite segregation. The corneous seeds of ears (10 x 5)-5 x (5-3)-7 and (10 x 5)-1 x (5-3)-3 were also tested. A total of 13 self-fertilized and 87 open field ears were pure corneous flints like the corneous flint parent, No. 5.

TABLE 5.

SELF-POLLINATED EARS OBTAINED FROM PLANTING FLOURY SEEDS OF EAR (10 x 5)-5 x (5-3)-7 AND EAR (10 x 5)-1 x (5-3)-3.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5) x 5-7S-6	102	116
" -5	125	137
" -1	77	48
" -8	126	110
" -2	128	106
" -7	67	36
(10 x 5) x 5-3S-2	93	58
" -8	74	71
" -1	126	92
" -6	96	76
Total	1014	850

Table 6 gives the results obtained from planting corneous seeds of ears (10 x 5)-13 x (10-3)-14. As these seeds were assumed to be the result of a cross between corneous and floury types, it was to be expected that all resulting ears would show segregation. Five self-fertilized ears evidently came from hybrid seeds as they gave a total ratio of 653 corneous to 620 floury seeds. Of 57 open field ears, 56 came from hybrid seeds. One ear which was somewhat immature probably was a pure soft floury ear. This result may be explained by assuming that one floury seed was planted by mistake.

Of the 7 self-fertilized ears obtained from planting the floury seeds of the cross between (10 x 5)-13 x (10-3)-14, all were pure floury. Of the open pollinated ears, 11 were unquestionably pure floury while 2 indicated segregation. These ears may have come from corneous seeds planted by mistake, although it is possible that a few stalks were mislabeled at harvesting time, as the stalks bearing the open pollinated ears all were shocked on the same field.

TABLE 6.

SELF-POLLINATED EARS OBTAINED FROM PLANTING CORNEOUS SEEDS OF EAR NO. (10 x 5)-13 x (10-3)-14.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5) x 10-3-14C-4	127	116
" " -9	200	172
" " -7	70	71
" " -6	73	94
" " -10	183	167
Total	653	620

Table 7, gives the results of planting seeds of Ear No. (5-3)-20, pure corneous flint, which was pollinated with pollen from F_1 generation cross (10 x 5). There was no immediate effect of the pollen of (10 x 5)-6 upon the pure flint ear (5-3)-20. Of 5 self-fertilized ears obtained from growing this cross, 4 showed segregation, giving a total of 528 corneous to 508 floury seeds, and 1 was pure corneous. Of the open field ears 24 were pure corneous and 34 showed segregation. These results show that the pollen grains carry the factors for corneous and floury starch in the ratio of 1 to 1.

Table 8 gives the results of planting seeds of ear (10-3)-13, which was pollinated with pollen from an F_1 ear (10 x 5)-14. There was no visible effect on the endosperm of (10-3)-13 due to crossing. Three of the self-fertilized ears obtained from this cross had a total of 397 corneous to 377 floury seeds; 6 self-fertilized ears were like the floury parent. Of the open field ears, 32 were homozygous floury and 30 were hybrids.

TABLE 7

SELF-POLLINATED EARS OBTAINED FROM PLANTING CORNEOUS SEEDS OF EAR NO. (5-3)-20 x (10 x 5)-6.

Ear Number	Corneous Seeds	Floury Seeds
5 x (10 x 5)-2	116	113
" -3	116	116
" -5	126	120
" -8	170	159
" -9	Pure corneous	
Total in hybrid ears	528	508

TABLE 8.

SELF-POLLINATED EARS OBTAINED FROM PLANTING FLOURY SEEDS OF EAR NO. (10-3)-13 x (10 x 5)-14.

Ear Number	Corneous Seeds	Floury Seeds
10 x (10 x 5)-6	158	156
" -7	84	79
" -4	155	142
" -1	Pure floury	
" -2	"	
" -3	"	
" -4	"	
" -5	"	
" -6	"	
Total in hybrid ears	397	377

Table 9 gives the results of planting the corneous seeds of (10 x 5)-8C-8 and (10 x 5)-8S-8. This F_3 generation was grown to determine whether a constant splitting into a 1 to 1 ratio in the hybrid ears could be expected. The results show no great deviations from this ratio. On 9 selfed ears showing segregation there were 996 corneous and 954 floury seeds.

The total progeny of (10 x 5)-8C-8 consisted of 12 hybrid ears and 15 corneous ears, while the progeny of (10 x 5)-8S-8C included 17 hybrid and 10 pure corneous ears. Considering the few individuals grown the data corroborate those of the previous generation.

TABLE 9.

SELF-POLLINATED EARS OBTAINED FROM PLANTING CORNEOUS SEEDS OF F_2 GENERATION EARS (10 x 5)-8C-8 AND (10 x 5)-8S-8.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5)-8C-8C-1	150	116
" -3	116	133
" -2	Pure corneous	
" -5	"	
" -7	"	
" -8	"	
(10 x 5)-8S-8C-1	114	132
" -2	96	115
" -4	103	98
" -5	142	104
" -6	114	95
" -7	89	101
" -8	72	60
" -3	Pure corneous	
Total in hybrid ears	996	954

Table 10 gives the results of planting floury seeds of ears (10 x 5)-8C-8 and (10 x 5)-8S-8. In 8 self-pollinated ears there were a total of 966 corneous and 997 floury seeds. Among the progeny of (10 x 5)-8C-8S there were 17 segregating ears and 16 floury ears, while the progeny of (10 x 5)-8S-8S gave a total of 12 segregating and 10 floury ears. The data in these two tables show that the progeny of an ear which is a cross between floury and corneous may be expected to give a ratio in F_2 of 1 corneous, 2 segregating to 1 floury ear.

TABLE 10.

SELF-POLLINATED EARS OBTAINED FROM PLANTING FLOURY SEEDS OF (10 x 5)-8C-8 AND (10 x 5)-8S-8.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5)-8C-8S-1	112	132
" -2	157	174
" -5	155	150
" -6	100	98
" -7	150	150
(10 x 5)-8S-8S-2	98	107
" -3	96	100
" -4	98	86
" -1	Pure Floury	
" -4	"	
(10 x 5)-8C-8S-8	"	
" -3	"	
Total in hybrid ears	966	997

To test the purity of apparently homozygous segregates the seeds of pure corneous ear (10 x 5)-8C-6 were planted. A total of 63 ears were all pure for the corneous habit. Pure floury ear (10 x 5)-8S-2 gave a progeny of 78 ears. All were of a similar character and contained seeds which were nearly filled with soft starch. There were traces of corneous matter in some seeds, but under Connecticut conditions the floury parent also produces traces of corneous matter in a few seeds.

SUMMARY AND INTERPRETATION OF RESULTS.

In general, no matter which variety was used as the female parent, there was no immediate visible effect of the male parent in the endosperm of crosses between No. 5 flint and No. 10 floury maize. The F_1 generation plants produced ears in which there was a clear segregation of corneous and floury seeds in a 1 to 1 ratio. This ratio was unaffected whether the F_1 ears were pollinated with pollen from either the pure flint or the pure floury parent. The progeny of a cross between F_1 and the flint parent gave a ratio of 1 hybrid ear to 1 pure flint ear. Likewise the progeny of a cross between F_1 and the floury parent gave a ratio of 1 floury ear to 1 hybrid ear. Seventy-six

F_2 ears produced from a self-fertilized F_1 ear of cross (10 x 5), gave a ratio of 1 pure flint ear, 2 hybrid ears and 1 pure floury ear. The flint and the floury ears bred true in later generations.

A total of 69 self-fertilized ears showing segregation gave a ratio of 8,803 corneous seeds to 8,562 floury seeds. This is a ratio of 1 to .961 or approximately 1 to 1.

The above results prove that the visible endosperm character of a seed shows the potentiality of the female gamete which entered into that particular seed, and that the male gametes have no immediate effect on the endosperm to determine whether they be corneous or floury. Data from later generations, however, show that the pollen grains of plants from hybrid seeds transmit both the corneous and the floury condition, approximately ½ carrying a factor for corneous seeds and the other half a factor for floury seeds.

Two hypotheses will explain the facts: either there is no fusion between the female endosperm nucleus and the so-called second male nucleus of the pollen grain, in which case the endosperm developes wholly from the endosperm nucleus of the embryo sac and therefore exhibits the gametic character of the egg cell; or, there is dominance of the condition of the mother. As ordinarily two female polar nuclei unite with a single male nucleus to produce the endosperm it might be expected that this double dose of the female character should predominate over a single dose of the male character, so that by inspection the seeds would be classed as of the mother type. Correns (1901) used the second hypothesis to account for certain results in his study of the inheritance of color in the aleurone cells, where there appeared to be a dominance of the maternal condition. Although East and Hayes (1911) were able to show that Correns' assumption was unnecessary in the case of aleurone color, the aberrant ratios obtained being due to the interaction of several factors, it does appear to fit the facts in the crosses just described.

A cross between a yellow corneous race and a white floury race would show the correct explanation of the results of the floury-flint cross, for if in F_2 the ratio of yellow to white was 3 to 1, and of corneous to floury, 1 to 1, it would then be

established that there was a fusion of the female polar nuclei with a male generative cell. Emerson suggested that the same test could be made by pollinating ears which were expected to give a 1 to 1 ratio with pollen from a yellow corneous flint. At the time this test was to be made no seeds of the immediate cross between the corneous and floury races were available, but a number of seeds of hybrid ears (10 x 5)-8C-8S-6 were planted and the resulting plants crossed with pollen from a corneous yellow flint known to breed true. Four ears were obtained of a cross between (10 x 5)-8C-8S-6C (the corneous seeds) and the yellow flint. They proved to be yellow corneous flints. Of the naturally pollinated ears obtained from (10 x 5)-8C-8S-6C, 12 were pure corneous flints and 18 hybrids. Five ears of (10 x 5)-8C-8S-6S (the floury seeds) were also pollinated with pollen from the yellow corneous race. All five ears were yellow and four were yellow floury ears. One ear was a definite hybrid, however, and gave a ratio of 55 floury seeds to 59 corneous seeds. Of the open field ears of (10 x 5)-8C-8S-6S, 13 were pure floury and 14 hybrids.

The ear which *had all yellow seeds* and yet showed a ratio of 55 floury to 59 corneous, seems sufficient evidence for concluding that the apparent dominance of the condition of the mother is due to the fact that the endosperm is produced from a union between two female polar nuclei and one male cell. Thus two doses of a flour corn factor dominates one dose of the corneous factor and *vice versa. This fact has an important bearing on the multiple factor hypothesis for interpreting the inheritance of quantitative characters, for it shows that a series of factors may have cumulative somatic effects.*

Family (10x6), Flour x Dent.

This cross was made in 1909 between self-fertilized strains of Leaming No. 6 and floury No. 10. An F_1 generation was grown in 1910, and an F_2 generation from the seeds of F_1 ear (10 x 6)-1 was produced in 1911. There was no appreciable effect on the physical condition of the starch in the seeds of No. 10 due to the pollen of No. 6. On the F_1 ears the seeds were in-

termediate between No. 10 and No. 6 in size, and were rather uniformly dented. As regards the appearance of the starch in the seeds, there was definite segregation, but classification was difficult due to the fact that all seeds contained soft starch at the cap and sides and were dented. The seeds of the self-fertilized F_1 and F_2 ears were all examined carefully against a strong light, however, and were classified as accurately as possible. The results of this classification are given in Table 11. Considerable variation in the ratios on the different ears is exhibited, but as a rule there is an indication of a 1 to 1 ratio.

Although this seed classification may not have been as accurate as might be desired owing to the difficulties involved, the division of the total population of F_2 ears into corneous, hybrid and floury types as shown in Table 12, is exact and serves as a complete corroboration of the theory. Thirty-six ears were classed as pure corneous, eighty as hybrids and thirty-seven as pure floury. This is certainly a close approximation of a 1:2:1 ratio.

An examination of the F_2 ears showed that there was considerable range of variation between the different ears which were classed as corneous or floury types. There was a little variation among the seeds of the same ear, but this was not greater than could be explained by differences in development due to physiological causes. The pure corneous or pure floury ears, however, differed from each other by a considerable amount, and it seemed likely that some of this variation would be inherited. Of the ears of Table 11, (10 x 6)-1-13, (10 x 6)-1-3 and (10 x 6) 1-4 bred true to the floury type.

The corneous seeds of ear (10 x 6)-1-5 produced 13 hybrid and 17 pure corneous ears, while the floury seeds yielded 19 pure floury and 16 hybrid ears. Corneous ear (10 x 6)-1-5-2 was grown the following year and produced dented ears which bore seeds containing a fair proportion of corneous starch.

Ears (10 x 6)-1-6, (10 x 6)-1-9, (10 x 6)-1-12 and (10 x 6) -1-14 of Table 11 were grown in 1912. All produced ears having seeds with a considerable proportion of corneous starch, the progeny of No. (10 x 6)-1-6 and No. (10 x 6)-1-12 having

about the same proportion, and of No. (10 x 6)-1-9 and No. (10 x 6)-1-14, having a greater proportion of corneous starch than the dent parent.

TABLE 11.

RECORD OF SELF-FERTILIZED EARS OF F_1 AND F_2 GENERATION OF CROSS BETWEEN NO. 10 AND NO. 6.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 6)-5	104	75
(10 x 6)-2	159	226
(10 x 6)-1-1	123	48
" "-2	157	152
" "-3a	199	145
" "-4a	307	250
" "-5	242	208
" "-6a	149	94
" "-7	199	182
" "-8	124	77
" "-9a	259	202
" "-10	226	196
" "-11	212	209
" "-12a	182	106
" "-13a	107	108
" "-14a	42	30
" "-15	72	85
" "-16	hybrid ear, immature	
" "-6	considerable corneous starch in all seeds	
" "-9	all seeds very corneous	
" "-10	some varibility, no seeds as No. 10 (variation probably due to immaturity)	
" "-11	pure corneous	
" "-12	pure corneous	
" "-14	all seeds very corneous	
" "-15	pure corneous	
" "-3	as No. 10	proved pure floury in 1912
" "-4	probably as No. 10	proved pure floury in 1912
" "-16	"	
" "-17	as No. 10	
" "-18	"	
" "-19	"	
" "-13	"	
" "-20	"	
" "-21	Probably as No. 10	
" "-22	"	
" "-23	"	
" "-24	"	
Total in hybrid ears	2863	2393

TABLE 12.

F_2 EARS OBTAINED FROM GROWING EAR (10 x 6)-1.

Parent Stock	Pure corneous	Hybrids	Pure Floury
[Hand pollinated ears]	7	16	12
Dark yellow seeds of (10 x 6)-1	11	16	8
Light yellow seeds of (10 x 6)-1	7	24	8
White seeds of (10 x 6)-1	11	24	9
Total	36	80	37

All ears obtained from ear No. (10 x 6)-1-9 selfed had small seeds with traces of dent. On some ears there were merely traces of dent, but other ears showed the dented condition in all seeds. Selections were made to determine whether these variations were inherited. In 1914 a self-fertilized ear which bore seeds with only a few traces of dent was grown, also an ear with all seed dented. The progeny of these ears is given in Table 13.

TABLE 13.

THE PROGENY OF EARS NO. (10 x 6)-1-9-1 AND (10 x 6)-1-9-2.

Condition of Parent Ear	Progeny Classes.			
	¾ seeds dented	½ seeds dented	Few seeds dented	No seeds dented
Few seeds dented	9	12	14	1
¾ seeds dented	11	7	20	3

These results show that little progress was made by the selection.

Of the self-fertilized ears obtained from ear No. (10 x 6)-1-14, one showed no trace of dent, all of the seeds containing a large proportion of corneous starch. This ear was grown and compared with another self-fertilized ear which showed traces of dent in nearly all seeds. The results are given in Table 14.

TABLE 14.

The Progeny of Ears No. (10 x 6)-1-14-1 and (10 x 6)-1-14-2.

Condition of Parent Ear	Progeny Classes		
	½ Seeds dented	Few seeds dented	No seeds dented
No seeds dented		4	27
Half seeds dented	5	11	19

In this case there seems to be some effect of selection, although the number of individuals grown is not very large.

Conclusions.

There seems to be a close agreement between the results of the cross between 10 and 6 and those reported for the cross between 10 and 5. It was, however, more difficult to classify the seeds in the (10 x 6) cross as in No. 6 corneous starch is produced only on the sides of the seed, the cap and the immediate vicinity of the embryo being filled with soft starch.

The essential difference between No. 10 and No. 6 in type of starch produced is evidently one factor, yet since different F_3 families showed variations in the amount of corneous starch produced, there must be several minor factors which modify its development. There is good evidence that at least some of these minor factors are factors which have a direct effect on totally different tissues. For example, the size and shape of the seed which is at least partly controlled by the type of pericarp (a maternal character) has considerable influence upon the appearance of the starch. To put the matter roughly, in plants which fundamentally have the same zygotic possibilities as regards the type of starch in the endosperm, the amount of soft starch actually developed is directly proportional to the size of the seed.

Family (10 x 64), Floury x Rice Pop (Very Corneous.)

The No. 10 parent had been self-fertilized for three years and the No. 64 parent had been self-fertilized for two years prior to 1909 when the cross was made. There was no visible effect of the pollen of No. 64 on No. 10. F_1 ears were grown in

1910, but in no case was there a clear segregation among the seeds like that occurring in the F_1 ears of crosses (10 x 5) and (10 x 6). This may have been due to the fact that the ears were somewhat immature. The seeds of three F_1 ears were separated into two classes; first, seeds as floury as No. 10; second, all remaining seeds. These partially corneous seeds showed a range of variation from very corneous seeds to those which contained only a little more corneous matter than the No. 10 flour parent. The result of this classification is shown in Table 15.

TABLE 15.

F_1 Ears of Cross Between (10 x 64).

Ear Number	Floury Seeds	Corneous Seeds
(10 x 64)-7	93	216
(10 x 64)-10	82	349
(10 x 64)-12	168	353
Total	343	918

The seeds of (10 x 64)-7 and (10 x 64)-10 were planted in 1911. Those which had been classed as of the floury type like No. 10 were planted as (10 x 64)-7S and (10 x 64)-10S. The remainder of the seeds of the same ears were planted as (10 x 64) -7C and (10 x 64)-10C respectively. The results obtained from a classification of the progeny of these ears are given in Table 16.

TABLE 16.

Ears Obtained From Planting (10 x 64)-7C and 7S and (10 x 64)-10C and 10S.

Parent Type	Progeny Classes				
	Pure Floury	Intermediate Floury	Definite Hybrids	Intermediate Corneous	Pure Corneous
(10 x 64)-7S	4	15	11	6	
(10 x 64)-10S	6	13	17	2	
(10 x 64)-7C			16	7	13
(10 x 64)-10C		1	15	6	10

There is a similarity in the variability of the populations obtained from the floury seeds of (10 x 64)-7S and (10 x 64)-10S; the progeny of the corneous seeds of (10 x 64)-10 and (10 x 64) -7 also show about the same percentage of ears in the different classes.

Two self-fertilized F_2 ears (10 x 64)-10S-5 and (10 x 64) -10C-4 were classed as definite hybrids. The corneous seeds of these ears gave a range of variation from purely corneous to definitely hybrid ears, there being 3.3 times as many corneous, intermediate, and definitely hybrid ears, as there were pure corneous ears. The floury seeds of (10 x 64)-10S-5 and (10 x 64)-10C-4 produced 4.2 as many hybrid and intermediate ears as pure floury ears. Thus these two F_2 ears showed as variable a progeny in F_3 as had been found in F_2.

Five self-fertilized F_2 ears of the intermediate floury class from the progeny of (10 x 64)-10S gave a total population of 165 ears; of which 19 approached pure corneous but contained a larger percentage of soft starch than the corneous parent, 12 approached the floury parent, and 134 were intermediate. Many of these intermediate ears showed some variation among the seeds, but no clear segregation.

F_2 corneous ears, (10 x 64)-10C-9, (10 x 64)-7C-9, and (10 x 64)-7C-1 bred true for the corneous habit in F_3. (10 x 64) -10C-9 was grown in F_4 and again bred true.

Pure floury ear (10 x 64)-7S-13 bred true in F_3 and F_4 for the floury habit.

One self-pollinated intermediate F_2 ear, (10 x 64)-7C-2 proved to be a hybrid and gave in F_3 15 corneous ears, 32 definitely hybrid ears showing clear segregation, and 18 intermediate corneous ears which showed some variation. This is a 1:2:1 ratio.

Two F_4 ears bred from the intermediate class, (10 x 64)-7C-2-10 and (10 x 64)-7C-2-1, together produced 14 ears approaching pure corneous, 68 intermediate variable ears and 4 approaching pure floury. These ears are probably all intermediates, the variation being due to maturity and possibly due to the effect of other inherited factors. Of 3 other F_2 ears classed as intermediate, 2 gave intermediate progeny and 1 proved to be a definite hybrid. Self-pollinated ears of selections (10 x 64)-7S-1 and (10 x 64)-7S-7 from the intermediate class were grown the following year. These results are given in Table 17.

TABLE 17.

PROGENY OF EARS NO. (10 x 64)-7S-1 AND (10 x 64)-7S-7 WHICH WERE CLASSED AS INTERMEDIATE VARIABLE EARS.

Ear No.	Parent type	Classification of Progeny		
		Approaching Corneous	Variable Intermediate	Approaching Floury
(10 x 64)-7S-1-2	Most corneous ear	2	35	
(10 x 64)-7S-1-6	" floury ear		40	1
(10 x 64)-7S-7-10	Intermediate ear	3	35	
" -2	"		48	
" -4	"		47	
" -8	"	2	‡46	

‡Of this population, 25 open field ears were very variable and showed definite segregation. The self-fertilized ears were comparatively uniform.

The data in Table 17 show that intermediate variable ears tend to give intermediate variable progeny. The ears did not all become thoroughly mature, and this may be the explanation of their variable endosperms. There is also the possibility that other heterozygous factors may have influenced development in such a way as to produce variation. (East & Hayes 1911).

F_3 ear (10 x 64)-10C-1-6 produced intermediate and corneous seeds in a ratio approaching 1:1. The corneous seeds of this ear gave a progeny of 28 purely corneous and 24 definitely hybrid ears, while the intermediate seeds gave a progeny of 2 corneous ears, 17 definite hybrids and 23 intermediate variable ears. This is a close approximation of a 1:2:1 ratio. That only 1 factor determined whether corneous or intermediate seeds were to be produced in this ear is further indicated by the separation of seeds from five self-pollinated ears which were classed as definite hybrids. The results are given in Table 18. The total number of corneous seeds in these five ears were 514 and of intermediate seeds 491. This clearly approaches a 1 to 1 ratio.

TABLE 18.

Classification of Seeds of Hybrid Ears Obtained From Planting Intermediate and Corneous Seeds of Ear (10 x 64)-10C-1-6.

Ear Number	Corneous Seeds	Intermediate Seeds
(10 x 64)-10C-1-6I-2	101	84
" -9	78	92
" -8	80	67
(10 x 14)-10C-1-6C-8	135	124
" -10	120	124
Total in hybrid ears	514	491

Summary and Interpretation of Results.

The pollen of No. 64 pop apparently had no effect on the character of the endosperm of No. 10 flour. This is in agreement with the results of the crosses (10 x 5) and (10 x 6). The F_1 ears showed the results of segregation, although in this case there was a range of variation from the floury to the corneous type. Seeds of this F_1 generation (F_2 seeds) produced a population of ears ranging from the pure corneous to the pure floury type.

One uniformly floury ear bred true in F_3 and F_4 for the floury habit; three ears with purely corneous seeds also bred true.

Two F_2 ears (10 x 64)-10S-5 and (10 x 64)-10C-4 gave as variable an F_3 progeny as had been found in F_2. The ratio in this case was approximately 1 pure corneous ear to 6.2 intermediates and definite hybrids to 0.8 pure floury ears.

Other F_2 ears gave a 1:2:1 ratio in F_3 as was the case in the (10 x 5) and (10 x 6) crosses. An example of such a ratio is that obtained from F_2 ear (10 x 64)-7C-2, which produced 15 corneous ears, 32 definitely hybrid ears and 18 intermediate ears.

Several self-fertilized intermediate F_2 ears bred comparatively uniformly, giving a progeny which contained more corneous starch than the No. 10 parent but less than the No. 64 parent. Thus intermediate ear (10 x 64)-7S-1 produced 41 ears of the intermediate type none being either purely corneous, definitely hybrids, or clearly floury. A self-fertilized ear (10 x 64)-7S-1-2 which contained more corneous starch than other self-fertilized

ears, yielded a progeny of 35 variable intermediate ears and 2 ears approaching the corneous condition although they were not truly corneous ears like No. 64. Self-fertilized ear (10 x 64)-7S-1-6 which approached the floury type, produced 40 intermediate variable ears and 1 ear with somewhat more floury matter, though it did not compare with No. 10. Thus in a total of 119 ears from this intermediate line (10 x 64)-7S-1 there were no pure corneous, pure floury or definitely hybrid ears. This variation may largely be due to differences in the maturity of the seeds and ears, as the amount of corneous starch is directly dependent on the maturity of the seeds, although of course the hereditary constitution determines the amount which can be produced under favorable conditions, but there is also considerable likelihood that what one may call minor inherited factors modify the expression of the character. Whether more than one major factor affecting the endosperm is involved is still a question. The ratio obtained among the progeny of ears (10 x 64)-10S-5 and (10 x 64)-10C-4, the facts that certain F_2 ears produced an F_3 progeny similar to the 10 x 5 cross, and that others bred approximately true to the intermediate, the pure floury, or the pure corneous types might seem to indicate two such factors, but analysis is so difficult that this is only a reasonable guess, as will be shown by a consideration of all of the facts.

The following conclusions we hold to be justified by the data at hand.

1. The factors directly responsible for the differences in the physical condition of the starch exhibited by the so-called starchy sub-species of maize, the flour, dent, flint and pop corns are as truly endospermal in their inheritance as endosperm color characters. They partake of the nature of the *embryo* and not of the *plant* on which they are borne.

2. These characters appear superficially to be maternal for the following reasons. The endosperm nuclei are triploid due to the fusion of two nuclei from the female gametophyte with one nucleus from the male gametophyte. In the characters under discussion, the presence of two factors always dominates the presence of one factor. Thus corneous female (CC) x floury male (F) is phenotypically corneous, while floury female (FF) x corneous male (C) is phenotypically floury. These characters,

therefore, *appear* to be inherited in a different manner from endosperm colors where the presence of *one* color factor is sufficient to cause perfect development of color. This is the first proof of a cumulative somatic effect of factors.

3. From the fact that in these crosses, as well as in numerous others involving the same subspecies of maize that we have examined, the F_2 reproduces the grandparental and no types more extreme than the grandparental types (with possibly a rare exception), it follows that a large series of multiple allelomorphs affecting the starchy condition of the endosperm exists.

4. From the facts (a) that where no complications such as differences in shape and size of seed exist (viz. cross 10 x 5) segregation is simple and definite, (b) that where such differences in shape and size of seed do exist segregation occurs but is difficult to demonstrate clearly until these complications have been eliminated, it follows that although only the presence of factors in the endosperm affect these characters directly, the maternal zygotic constitution has an indirect effect. This effect is roughly a direct correlation of size of seed with floury condition of the endosperm.

Having these facts in mind, let us see what difficulties obstruct analysis if it be assumed that two factor differences may differentiate the endosperms of certain maize varieties in respect to starch as seemed possible in the case of cross (10 x 64).

The simplest assumption would be that each of these factors has a similar effect, and when one sees the difficulties thus involved, and considers that such a simple assumption is less probable than one in which each factor has a different effect, it is clear why we do not wish to assert dogmatically that two such factors are involved in the cross between the flour and the pop-corn.

Let the flour corn be AABB and the pop corn aabb, it being understood that the phenomenon of dominance is in this case wholly a quantitative reaction. The F_1 generation in the cross and its reciprocal would be

AAa BBb
and
aaA bbB

In each case, the predominant influence of the mother would be such that any effect of the father would scarcely be noticeable. Four types of gametes would be formed in the F_1 generation as usual, AB, Ab, aB and ab,—but the appearance and breeding qualities of the zygotes formed would be peculiar, as is shown in the following table, due to the fact that the "gametes" of the embryo sac are the fusion cells AABB, AAbb, aaBB and aabb.

1 AAABBB	
1 AAABBb	Appear alike breed differently
1 AAaBBB	
1 AAaBBb	
1 AAAbbB	
1 AAAbbb	Appear alike breed differently
1 AAabbB	
1 AAabbb	
1 aaABBB	
1 aaABBb	Appear alike breed differently
1 aaaBBB	
1 aaaBBb	
1 aaAbbB	
1 aaAbbb	Appear alike breed differently
1 aaabbB	
1 aaabbb	

The grandparental types have appeared of course and will breed true, but other individuals will look like the grandparents though they will breed differently and will ultimately give the whole series if crossed together. Other complications will occur to any one who takes the trouble to study the table.

Family (65 x 64), White Pearl Pop x White Rice Pop.

In 1910 a cross was made, between white rice pop No. 64 and pearl pop No. 65 for the dual purpose of determining the probable value of such a cross for the commercial production of first generation hybrid pop corn, and to study the inheritance of the pointed seed characteristic of the rice pop corns.

The F_1 plants were considerably more vigorous than either parent. The seeds produced approached the length of those of the longer type, the white rice pop, and the width of those of the

broader parent, the pearl pop. Thus the F_2 seeds (those borne on F_1 plants) were considerably larger than those of either parent, and since the pericarp was weaker rather than stronger than that of the pure types, they did not pop as well.

TABLE 19.

INHERITANCE OF SEED SHAPE IN A CROSS BETWEEN WHITE RICE POP NO. 64 AND PEARL POP NO. 65.

Ear Number	Parent Type	Condition of Progeny: Pure Point	Inter-mediate Point	Non Point	Ratio of Pointed ears to intermediate and non point
64-4	Pure pt.	147			
65-8	Non pt.			200	
(65 x 64) F_1			132		
(65 x 64)-1 F_2	Int. pt.	6	64	1	1:10.8
" -3 "	"	5	49	5	1:10.8
" -5 "	"	9	55	3	1:6.5
" -6 "	"	4	58	2	1:15
" -1-13 F_3	Int. or non pt.		*21		

* Possibly non-point as the point was scarcely perceptible.

The data on the cross are given in Table 19. The F_1 generation was of intermediate habit,—there being some projection of the seeds at the point of attachment of the silk. Four selfed F_1 ears furnished F_2 generations. The progeny of these ears was variable, the seeds of some ears being as completely pointed as the white rice pop parent, the seeds of others non-pointed like the pearl pop parent, while the greater number were of various intermediate types. Of a total progeny of 263 individuals, 24 ears were classed as pure pointed like the white rice parent. This is an indication of a 15:1 ratio, although one can not be certain that the classification was correct because these ears were not selfed and could not be tested by the type of progeny produced. A number of F_2 ears were self-pollinated, but none happened to be obtained which could be classed as typically pointed. One

ear having seeds but slightly pointed (possibly non-pointed) was grown in F_3. The twenty-one ears produced were like the parent ear, showing only slight projections on the seeds at the tip of the ear.

The difference between the pointed seed characteristic of the white rice pop corn and the normal shape of seed typical of other varieties can not be explained by a single factor. If, however, we assume that there is a difference in two factors, that each factor is allelomorphic to its own absence and is inherited independently of the other, that both are necessary for the production of the pure pointed condition, and that either of them alone may produce a tendency to a pointed condition (intermediate point), the data accord fairly well with the theory. But since on this hypothesis it is assumed that a factor in the heterozygous condition, produces only half as great an effect as when homozygous, one can appreciate the difficulty of classifying the ears correctly by inspection, and since classification must be exact to prove such a case merely by the ratios obtained it must be admitted that our evidence is open to some criticism. On the other hand, we believe that the facts are clear enough to make them of some value in practical plant breeding, and we do not believe that the case is sufficiently important to make it worth while overcoming the difficulties that stand in the way of a more acceptable proof. Furthermore, the data on the next cross appear to corroborate our earlier facts.

Family (64 x 6), White Rice Pop x Leaming Dent.

This cross was made in 1909 between self-bred Leaming and white rice pop strains. The purpose of this cross was a further study of the mode of inheritance of quantitative differences in seed size, of the proportion of corneous to soft starch, and of the pointed habit of the white rice pop.

The results on inheritance of seed shape are given in Table 20. These results again indicate that two factors are involved. Furthermore, examination of Table 20 and Table 21, shows that the pointed character is inherited independently of the position of starch in the seeds.

TABLE 20.

INHERITANCE OF SEED SHAPE IN A CROSS BETWEEN NO. 6 LEAMING DENT AND NO. 64 WHITE RICE POP.

Ear Number		Parent Type	Condition of Progeny		
			Pure Point	Inter-mediate Point	Non Point
64-4	P_1	Pure pt.	147		
6-3-4	P_1	Dent non pt.			107
6 x 64	F_1			112	
(6 x 64)-4	F_2	Int. pt.	47	65	20
" -6	F_2	"	35	44	17
" -6-6	F_3	Pure pt.	26		
" -6-3	F_3	"	21	2	
" -4-8	F_3	Pure (?) pt.	44	20	
" -4-9	F_3	"	41	11	
" -6-4	F_3	Int. pt.	4	44	1
" -4-6	F_3	"	13	31	
" -4-4	F_3	"	13	37	2
" -6-5	F_3	Non pt.	4 (?)	53	4
" -6-7	F_3	"	3	34	
" -4-3	F_3	"	2	41	17
" -4-7	F_3	"	11	45	7
" -4-10	F_3	"		52	13
" -4-5	F_3	"	6	37	3
(6 x 64)-6-6-4	F_4	Pure pt.	35		
" -6-6-1	"	Pure or int. pt. (?)	27a		
" -4-8-8	"	Pure pt.	61b	1 (?)	
" -6-3-6	"	"	43		
" -6-5-4	"	Int. pt.	1 (?)	38	5
" -6-5-3	"	"	1 (?)	35	11
" -6-7-8	"	"	26	11	
" -4-8-3	"	"	16	40	
" -4-3-7	"	"	5	72	
" -4-10-5	F_4	"		47	22
" -4-10-3	F_4	Non or int.		48	17
" -4-3-5	F_4	Non			60

a—4 ears with points not as strongly developed as the remaining ears.
b—1 ear with points not as strongly developed as the remaining ears.

The F_1 generation was intermediate as regards the pointed condition, and there was segregation into pointed, non-pointed and intermediate ears in F_2. Thirteen self-pollinated F_2 ears were grown in F_3. Of these, the following F_2 ears were classed as pure pointed, (6 x 64)-6-6, (6 x 64)-6-3, (6 x 64)-4-8, (6 x 64) -4-9. Two of these ears, (6 x 64)-6-6 and (6 x 64)-6-3, bred true in F_3, while (6 x 64)-4-8 and (6 x 64)-4-9 showed segrega-

tion in F_3 with a total of 85 pointed and 31 intermediate pointed ears. Two self-fertilized ears, (6 x 64)-4-8-8 and (6 x 64) -4-8-3, were grown in 1914. One proved to be a pure pointed ear and the other again gave pure pointed and intermediate pointed seeds. These results might have been obtained if ear (6 x 64) -4-8 were homozygous for one factor for point and heterozygous for a second factor.

Three self-fertilized F_2 ears of the intermediate class showed a range of variation in F_3 from pure pointed to non-pointed ears. Six F_2 ears classed as non-pointed were proved to have been hybrids by the F_3 results. One of these, (6 x 64)-4-7, produced 52 intermediate and 13 non-pointed ears. As no typically pointed ears were obtained it seems fair to conclude that the parent ear (6 x 64)-4-7 was heterozygous for 1 factor for pointed seeds.

Two self-fertilized F_3 ears of line (6 x 64)-6-6 which bred true for the pointed habit in F_3 were grown in F_4. Ear (6 x 64) -6-6-4 gave a progeny of 35 ears, all of which were pure pointed; while (6 x 64)-6-6-1 had a progeny of 23 pure pointed ears and 4 with points more strongly developed than the intermediate class, but not so strongly developed as the 23 pure pointed ears. This may be a physiological variation or it may possibly be due to chance pollination. As these four were open field ears, it is impossible to determine the matter by further breeding.

The results are an excellent illustration of the old Vilmorin Isolation Principle,—in modern times the genotype hypothesis,—for they show that the only sure method to determine the breeding value of an ear is to grow and examine its progeny. A part of the pure pointed class gave a pure pointed progeny; other ears proved to be hybrids. There was also considerable difference in the progeny of different intermediate ears; some being apparently homozygous for one factor for point and heterozygous for another, while others appeared to be heterozygous for a single factor.

These results, as did those in the case of the (65 x 64) cross, indicate that two factors are involved in the production of strongly pointed maize seeds.

Table 21 gives the results of a study of the dented condition and the proportion of corneous to floury starch in the same

cross. The white rice pop parent contains only a small amount of floury starch, while the dent variety has corneous starch at the sides of the seed and floury starch at the cap and next the embryo. There was no effect on the development of the amount of corneous starch in No. 6 dent due to the pollen from No. 64 pop. The F_1 generation cross produced ears with intermediate sized seeds. These ears would have to be classed as dents.

TABLE 21.

INHERITANCE OF DENTED HABIT AND PROPORTION OF CORNEOUS TO FLOURY STARCH.

Ear Number		Parent Type	Condition of Progeny				
			Pure dent	Nearly pure dent	Half seeds dented	Few seeds dented	Non-dented
64-4		pop, non-dent					107
6-3-4		dent	147				
6 x 64 F_1				112			
(6 x 64)-4 F_2		nearly pure dent	15	27	27	20	3
"	-6 "	" " "	38	34	21	8	
"	-4-4 F_3	pure dent	29	1	15	5	1
"	-4-5 "	" "	1	11	24	6	
"	-4-8 "	" "		39	9		
"	-6-6 "	" "	24		2		
"	-6-5 "	" "	25	19	13	4	
"	-6-7 "	nearly pure dent	3	11	15	5	2
"	-6-4 "	" " "	2	2	35	8	2
"	-4-7 "	half seeds dented	14		24	5	3
"	-4-9 "	" " "	30	3	8	2	
"	-4-6 "	few seeds slightly dented		12	7	11	14
"	-6-3 "	" " " "	2	2	35	8	2
"	-4-10 "	non-dented				17	48
"	-4-3 "	" "				26	34
"	-6-3-6 F_4	pure dent	2	5	12	21	2
"	-6-5-3 "	" "	32	1	4		
"	-6-5-4 "	" "	6	23	12	3	
"	-6-6-1 "	" "	2	3	9	12	1
"	-6-6-4 "	" "	15	14	4	2	
"	-6-7-8 "	half seeds dent		1	4	9	23
"	-4-8-8 "	half seeds slightly dent		6	21	16	18
"	-4-8-3 "	seeds slightly dent		4	28	12	13
"	-4-3-7 "	few seeds dent		1	8	29	40
"	-4-3-5 "	no seeds dent				5	44
"	-4-10-5 F_4	few traces of dent				5	63
"	-4-10-3 "	non-dent					67

Two F_1 ears (6 x 64)-4 and (6 x 64)-6 were grown in F_2. Both populations showed a wide range of variation. The ears were classed as pure dent, nearly pure dent, half seeds dent, few seeds dent and non-dent. Ear (6 x 64)-4 had progeny of each class, while (6 x 64)-6 produced progeny in all classes except the non-dent class. Thirteen F_2 ears were grown in F_3. Two non-dented ears gave a progeny of non-dented ears and ears with a few seeds slightly dented. No ears bred true in F_3 or F_4 for the pure dented condition, although some selections gave a progeny with a much larger proportion of dented ears than others.

Twelve F_3 ears were grown in F_4. Ear (6 x 64)-6-5-3 produced the greater proportion of its progeny in the pure dent class. Ear (6 x 64)-4-10-3 bred true to the non-dented character, and the corneous non-pointed condition. Ear (6 x 64)-6-5-3 bore seeds which approached the size of those of the No. 6 Leaming parent, although the range of variation was somewhat greater. Ear (6 x 64)-4-8-3 gave a uniform progeny in 1914, and bred comparatively true to the seed size of the pop parent.

The seeds of those ears which were classed as non-dents and those with a few seeds dented, popped perfectly when tested. The condition of the other families is shown in the table.

Summary and Interpretation of Results.

The data from these two crosses indicate strongly that two independently inherited factors are necessary for the production of a strongly pointed seed. The rice pop point can be transferred from the pop parent to dented seeds by crossing and selection; the inheritance of these characters being entirely independent of each other.

A study of the proportionate amount of corneous and floury starch in the 6 x 64 cross shows a wide variation in F_2. One ear (6 x 64)-4-10-3 bred true for about the same amount of corneous starch in F_4 as that of the No. 64 parent. Other ears were again as variable as F_2, while still others showed a smaller range of variability. It is impossible to state how many factors are involved in producing these somatic differences, but it is a fact that the parental types can be recovered easily and will breed true.

Conclusion.

Since a summary of the results obtained for each cross has been given in its proper place, it seems unnecessary to repeat them here. If the reader will refer to them he will find an abstract of the paper.

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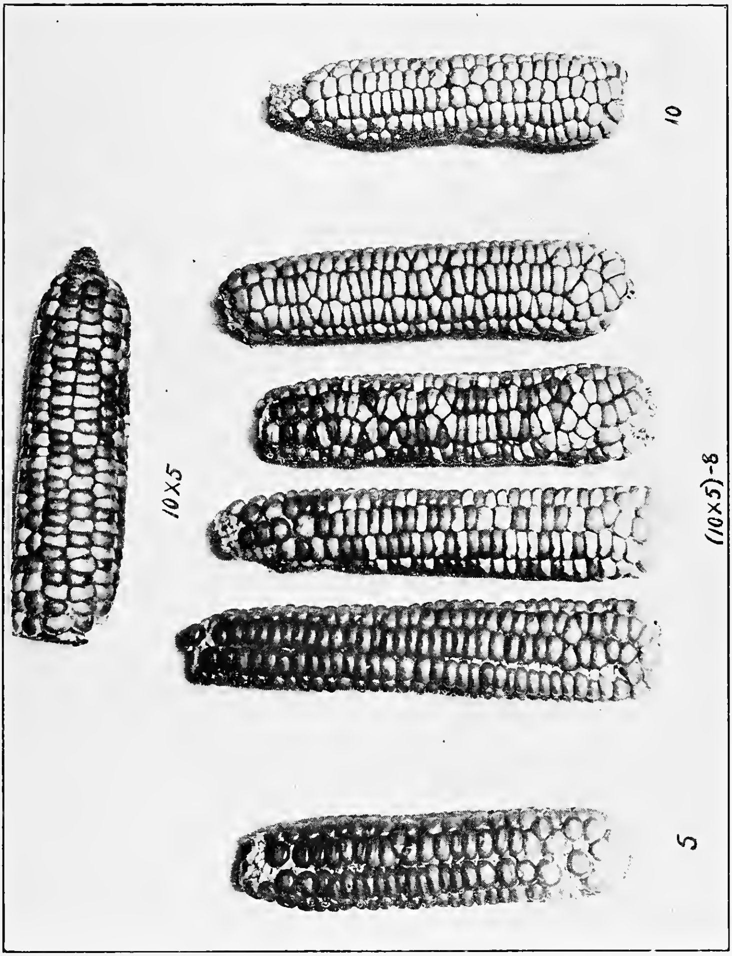
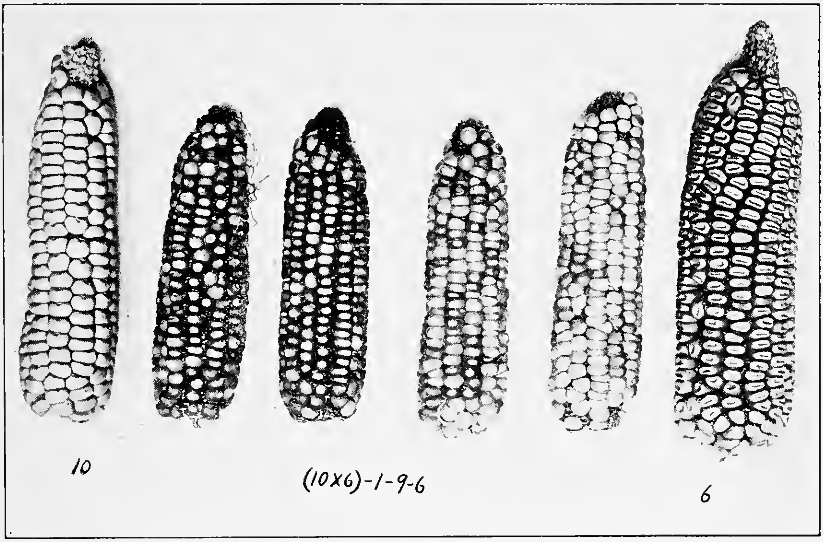
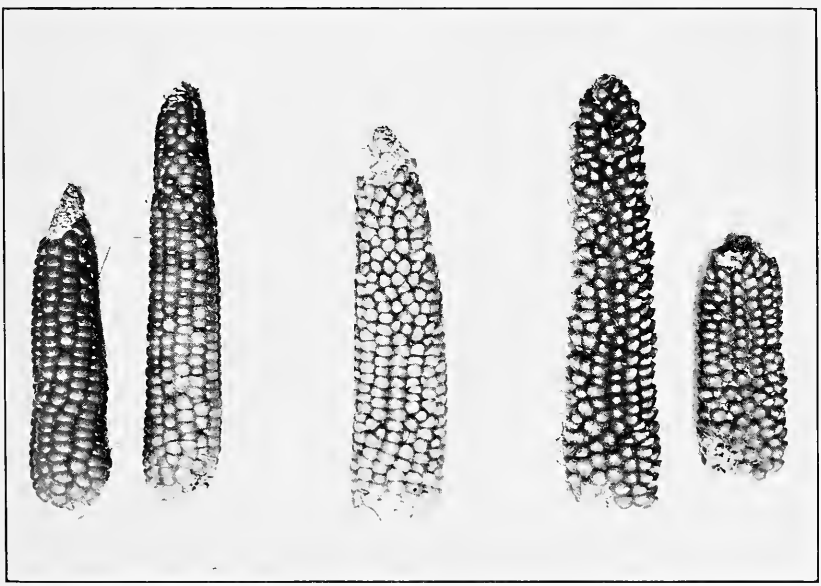
PLATE I.



No. 5, corneous flint at bottom, No. 10 flour at top and F_1 at left. The two lower center ears show the result of planting corneous F_1 seeds and the two upper center ears show the result of planting floury F_1 seed.

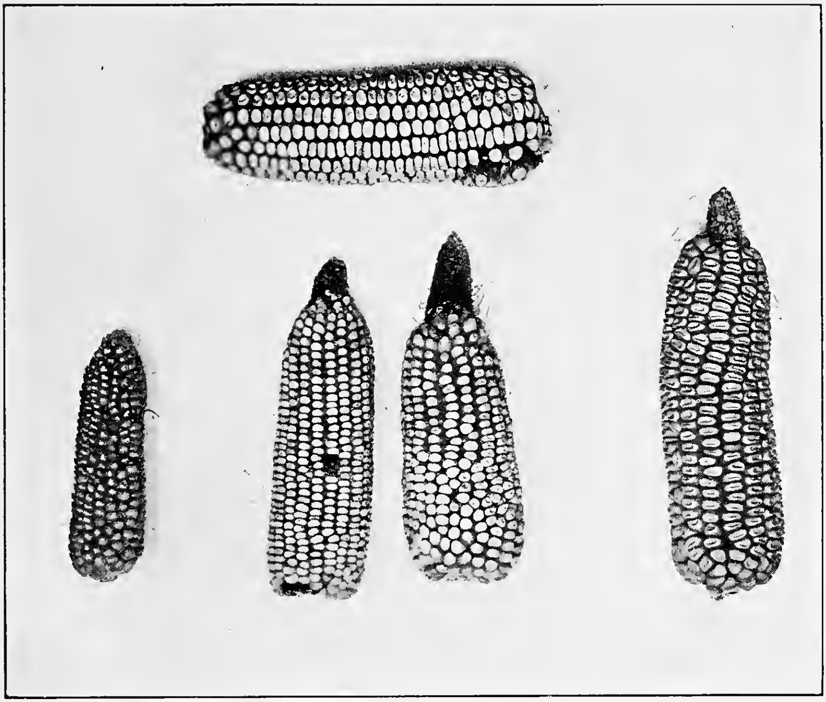


a. No. 10 flour at left. No. 6, Leaming dent at right. The four other ears represent the F_3 generation of cross. They are uniformly very corneous with slight traces of dent. The seeds are smaller than those of either parent and of uniform size.

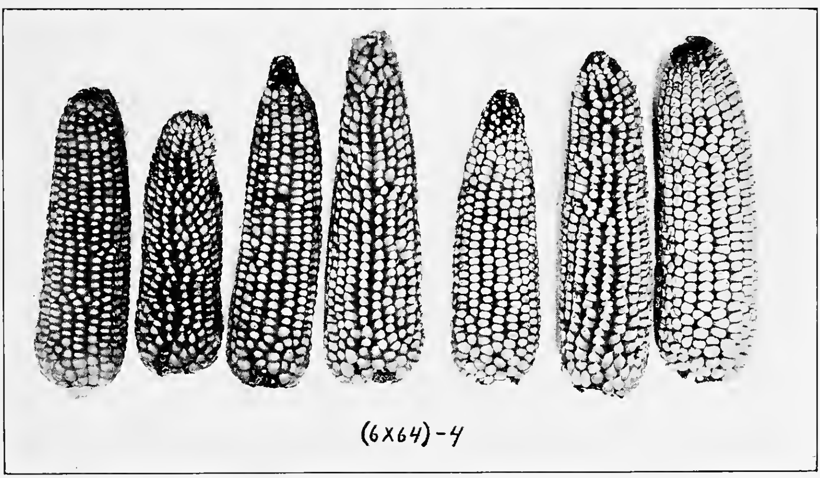


b. Average ears of No. 65 pearl pop at left, No. 64 rice pop at right with average F_1 in center. The two remaining ears represent the extremes of F_2.

PLATE III.

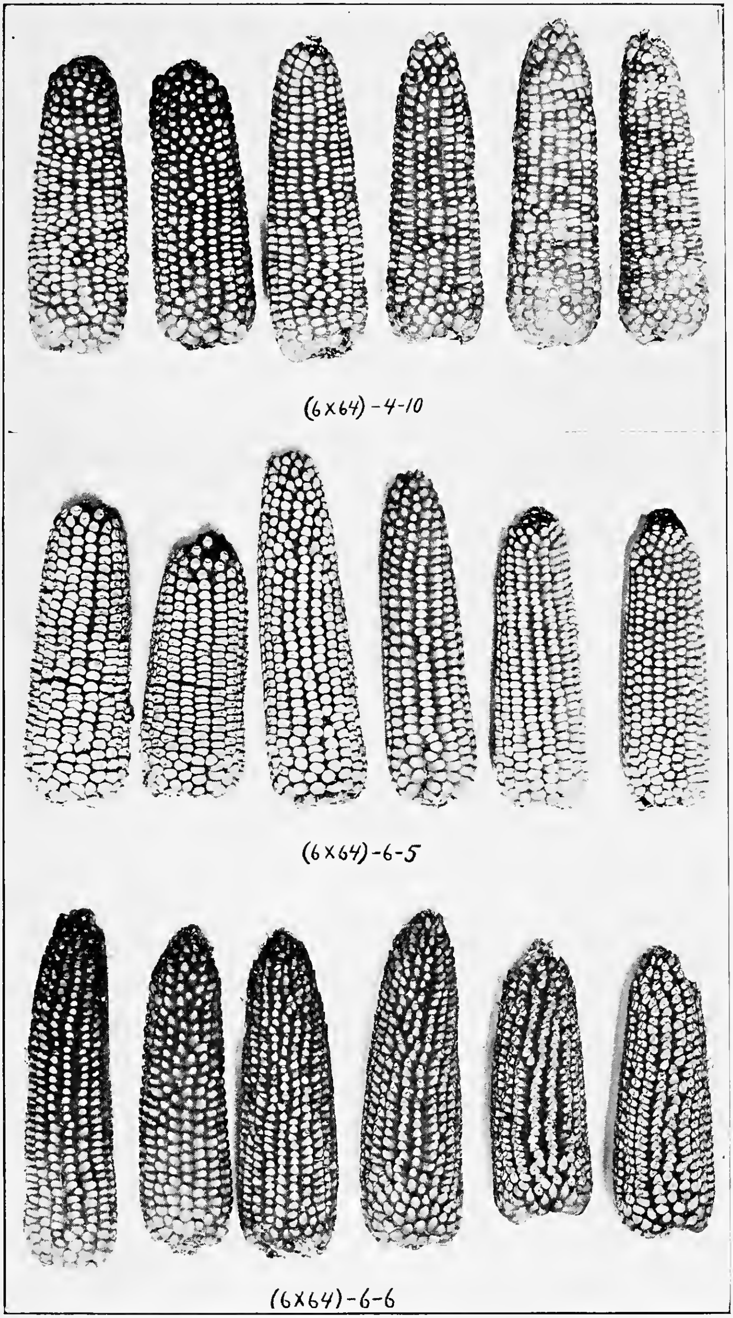


a. No. 6 Leaming dent at right, No. 64, rice pop at left and immediate cross, (6 x 64), above. The two central ears show the variation in seed size and condition of point of the F_1 generation.



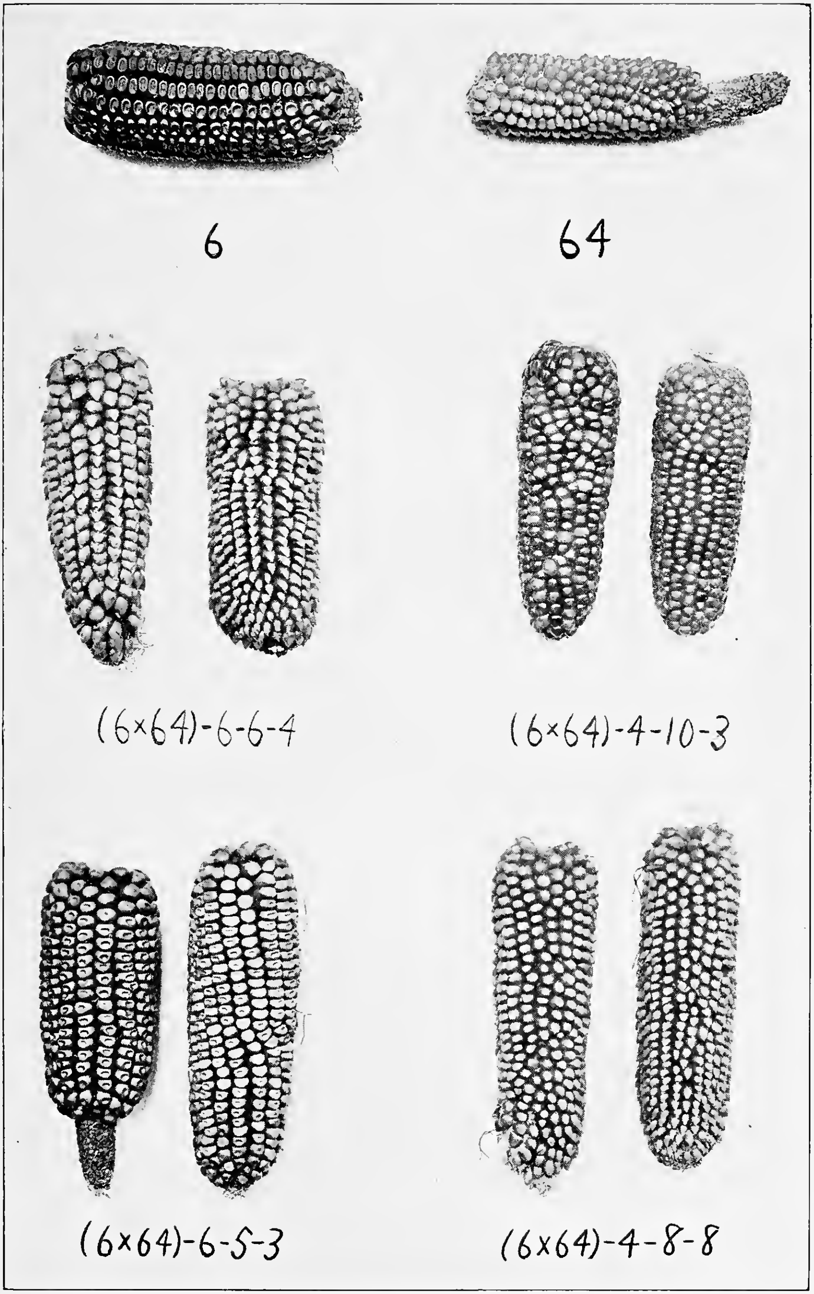
b. F_2 generation of cross (6 x 64). Note the segregation of characters.

PLATE IV.

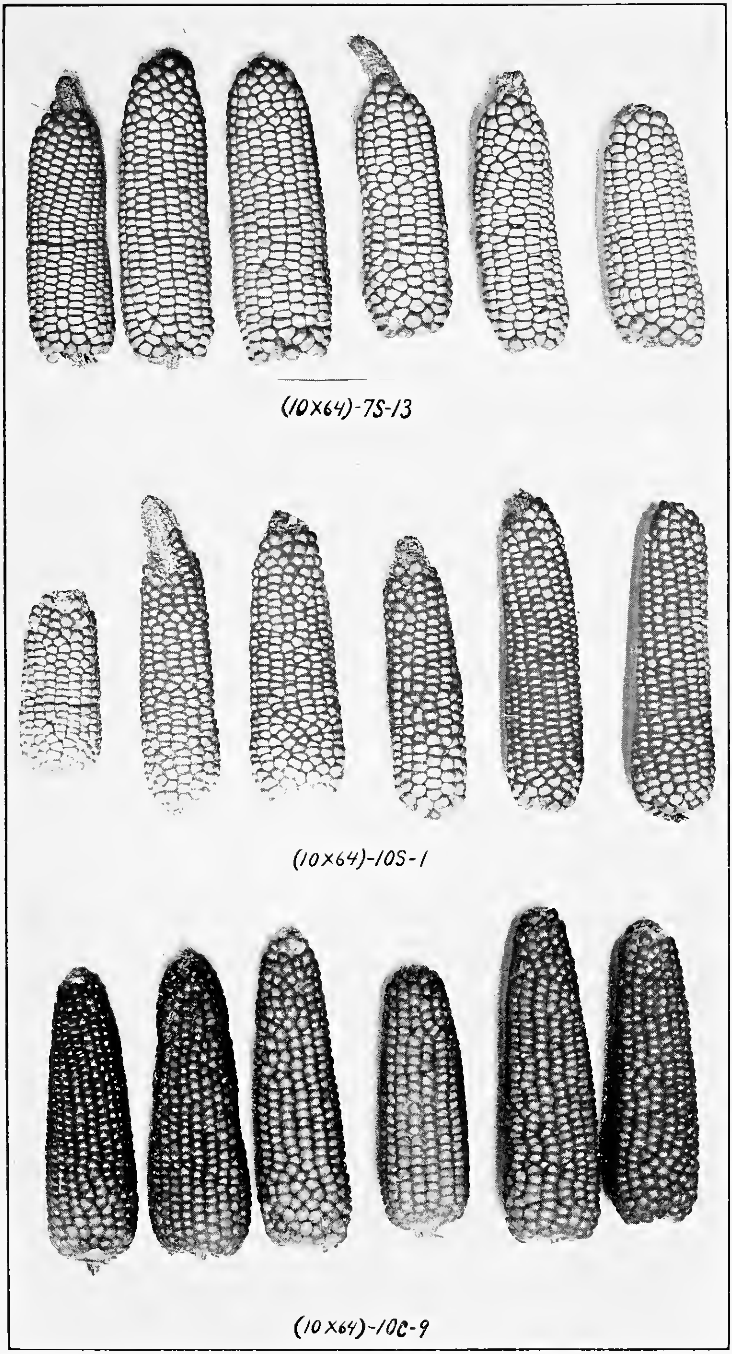


Upper row, F_3 generation ears, with large amount of corneous starch. Some ears with slight trace of dent. Middle row, average progeny of F_2 ear which bore good sized dented seeds. Lower row, average progeny of F_2 ear which bore intermediate dented seeds with a well-developed point.

PLATE V.



Average ears of parental types No. 6, Leaming dent and No. 64, white rice pop above. The ears below represent the variation in 4 F_4 families. (6 x 64)-6-6-4 bred true for the rice point, (6 x 64)-4-10-3 bred true for corneous, non-dented seeds, (6 x 64)-4-8-8 is a small-seeded selection and (6 x 64)-6-5-3 is a large-seeded selection. (Photo by Walden.)

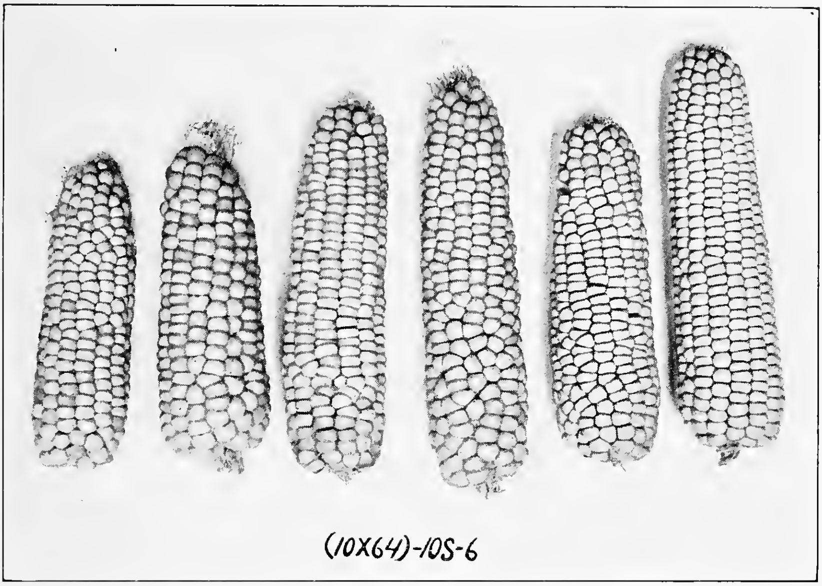


Upper row, F_3 generation of cross between No. 10 flour and No. 64, rice pop, which bred true for the floury habit.

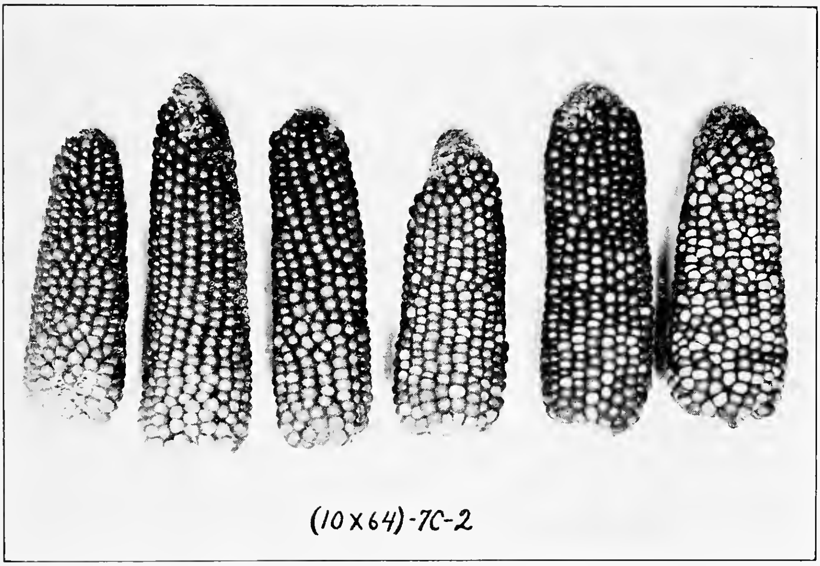
Middle row, F_3 generation of same cross which bore seeds of intermediate type.

Lower row, F_3 generation of same cross which bred true for the corneous habit.

PLATE VII.



a. F_3 generation of cross between No. 10 and No. 64 which bred true for the seed size of No. 10.



b. F_3 generation of cross between No. 10 and No. 64 which bred true for the seed size of No. 64. The corneous seeds popped perfectly.